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THE MECHANISM OF ROOT PRESSURE AND ITS RELATION TO SAP FLOW¹

JAMES BERTRAM OVERTON

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The important rôle played by osmotic pressure in plants is well recognized. Plant physiologists assume that osmotic pressure in the peripheral cells of the root is in some way connected with the process by which sap is continuously supplied to the xylem vessels, and the complex conditions controlling the movement of water from the soil through the root to the vessels are passed over by the use of the phrase "root pressure." Most of us are familiar with the contributions of Dixon, supported by the rather brilliant work of Renner, that water passes through the roots to the leaves because the leaves tend to dry out due to water being abstracted from them by evaporation, resulting in the water in the vessels passing into a state of tension, which is transmitted equally in all directions. This condition obtains unless root pressure or atmospheric pressure or both is forcing water up the stem more rapidly than it evaporates.

The cohesion theory of sap flow has received much attention and has been supported by considerable evidence. Transpiration or growth appears to produce an increase in the "saturation deficit" (Renner) or "incipient drying" (Livingston) in the exposed leaf cell walls which is followed by a corresponding increase in the saturation deficit in all the cells abutting upon the intercellular spaces of the leaf. Dixon points out that this condition is a sufficient cause for the entrance of water into the root and its passage through the root periphery. Renner has shown that the water-absorbing power of the root is directly related to the saturation deficit in the leaves above, and that the root's absorbing power appears to be directly referable to the tendency of the exposed cell walls of the root to dry out on account of passage of water to other parts of the plant. According to his view, during transpiration the root is rendered flaccid and therefore able to absorb water, although root pressure and passive absorption may under certain conditions work in combination.

Dixon holds that the entry of water into the root depends upon the gradient of pressure as we pass from the outside of the root to the inside of the tracheae, there being a fall of pressure due to the continuous water all the way up the stem to the leaves; thus the flow of water up the highest trees is due to the evaporation and condensation produced by the difference between the vapor pressure in the soil spaces and that obtaining around the

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leaves, and the tensile water flows under the action of this difference from end to end of the plant. The tensile stress transmitted to the root has the ultimate effect of drying out the root surface, and the gradient of pressure, which causes the passage of water from the soil into the root, is referable to the concave menisci formed in the cell walls of the root periphery due to the tension in the sap.

According to the above-outlined picture it would appear that in the absence of root pressure the passage of water from the soil into the root periphery is purely passive, the root acting merely as a filter in water intake, a view, however, to which Jost raises objections, although it has been shown that much water may be taken in by dead roots and that roots of transpiring plants can absorb water from solutions of high osmotic pressures. Concerning the mechanics of root absorption, however, we know comparatively little on account of the difficulties of observation, and little is actually known about the forces which are operative in the passage of water from the soil through the root into the vessels in sufficient quantity to supply the transpiration needs.

Root pressure is not generally considered as important in causing the ascent of sap through the stem. The presence of a negative gas pressure in the vessels shows that the water is not being forced up from below, and root pressure is lowest when transpiration is most active and highest when water movement in the stem is slowest. Dixon regards the function of root pressure to be a periodic flooding of the vessels with water, tending to bring the gas bubbles into solution and to reëstablish conditions for tension throughout the water tracts, the influence of root pressure in sap flow being an indirect one. The importance of osmotic phenomena in the root as far as water is concerned remains to be determined. It has been suggested by Livingston and Pulling that root pressure is mainly effective in maintaining the form of the roots and their contact with the water films of the surrounding soil. It has been shown that the rate of water absorption by roots is not proportional to the osmotic pressure of the root cells and that they can operate equally well with high or low turgidity so long as they are not deformed.

The exudation of liquid water from passive hydathodes, such as in *Colocasia*, and the secretion of water and solutes from wounds, show that the roots of many plants under certain conditions can develop considerable pressure. Whether or not it is admitted that sap pressure functions in sap flow, it seems certain that root cells are able to take in water and solutes and to pass them on to the xylem. Atkins holds that the cortical cells of the root have a much higher osmotic pressure than the tracheae and that they function as a complex semi-permeable membrane. It is evident that sap pressure, whether in roots or elsewhere, depends upon osmotic phenomena. It would appear from a survey of the literature that sap movement in roots is to be explained in the same way as the action of glands and hyda-

thodes, and that there exists the unilateral secretion of water and solutes from the root parenchyma into the vessels, which is an osmotic phenomenon. The question arises as to how such a unilateral excretion can take place from a turgescent cell.

Pfeffer first pointed out the necessity of investigating experimentally the secretion of water and solutes in one-celled plants as a basis for understanding the phenomena in hydathodes. This Lepeschkin has done, and on the basis of experiments he explains the continuous secretion of water and solutes by *Pilobolus* by assuming a different semi-permeability on the upper and lower sides of the cell. He finds that the lower or absorbing part of the sporangiophore may possess a greater osmotic pressure than the upper or secreting portion, and adopts Pfeffer's assumption that, if the cell sap at different points in the cell has different concentrations, the inflow must exceed the outflow until an equality is reached between the sides, so that there results a unilateral exudation of water through the upper, more permeable, membrane, brought about by a pressure corresponding to the difference in concentration on the two sides of the cell. The same holds true for the epidermal secreting structures of phanerogams and ferns.

Pfeffer's scheme assumes an unequal distribution of osmotic material in the protoplasm, the concentration being greatest in that part of the cell which is richest in osmotic substances. Lepeschkin has actually determined that such a condition obtains in *Pilobolus*, which indicates in this case that the two opposite ends of the cell are chemically and physically different. We should, therefore, expect that the water-absorbing and the water-holding capacity of the two sides of the cell would be different. Copeland actually constructed a piece of apparatus by which a current of water is maintained through an artificial cell by using membranes unequally permeable, thus proving Pfeffer's assumption, and holds that it is possible for the osmotically active substances in a cell to exert different pressures in different directions if the protoplasm is permeable to these substances in different degrees in different parts. Copeland points out that root pressure must be due to the same process, and that in order for root pressure to be caused in this way the protoplasm must be permeable to the osmotically active matter of the cell sap to a different degree in different parts of itself.

On the basis of Lepeschkin's results and of some of his own, Priestly recently attempts to explain the movement of water and solutes through the root and their excretion into the xylem vessels. He points out, as has been suggested by Atkins, that on account of sugar being brought down from the leaves by the vascular elements, the sap of the cells bordering on the vessels will tend to be more concentrated than that of the cells further out, and an osmotic gradient will be established from these cells through the root parenchyma to the root periphery. As a result of this osmotic gradient, water will enter at the periphery and pass toward the center, gradually distending the cells of the parenchyma of the vascular cylinder.

The parenchyma within the endodermis, being confined, is limited in extensibility on account of the structure of the endodermal cells. A strong hydrostatic pressure will therefore develop in this core of cells, sufficient to cause an excretion of water and solutes into the xylem vessels so long as the osmotic gradient obtains. When the water and solutes enter the xylem they are free to move upward in the vessels. Water may leak backward as far as the endodermis but no further on account of the suberized walls of the endodermis, which structure has been shown to prevent such a backward leakage. Priestly shows that the apical region of the root does not permit a backward leakage.

This explanation of root absorption and secretion offers some difficulties. Priestly points out that it is difficult to understand how the necessary solutes can be provided in sufficient quantities to permit a constant flow of water across the inner membranes of the cells next to the xylem vessels, where a considerable amount of water may pass upward. On the basis of Lepeschkin's results, Priestly suggests that such solutes might be either organic or inorganic, and that in the root they are organic, either sugars or, more probably, organic acids derived from sugars, and cites Atkins' results as to the presence of sugar in the ascending sap. Curtis, however, holds that the xylem does not serve for longitudinal translocation of carbohydrates.

In harmony with Bayliss, Priestly suggests that normal semi-permeability to glucose is a function of the difference in concentration on the two sides of the membrane, so that an accumulation or a dilution of sugar within the cells bordering on the xylem vessels might lead to a change of permeability in these cells and result in rendering the plasma membrane on the inner side temporarily permeable to sugar, and thus in an intermittent excretion into the xylem vessels. As Priestly suggests, the process, although intermittent, would appear as a continuous one in root pressure, due to the combined activity of many cells.

Flood finds that the exudation of water from *Colocasia* leaves does not depend upon any special secretion tissue in the leaves, but that the phenomenon rests upon the action of cells lower down, probably in the root. During its passage upward from the roots until its exudation, the water passes through no filtration membranes. The water exuded is almost free from solutes as has been shown by Atkins. If we assume that solutes are excreted into the xylem along with the water, the question arises as to what becomes of these solutes in the case of *Colocasia*. Priestly suggests that they are adsorbed during their passage upward by the protoplasts surrounding the vessels.

Transpiration has by some been looked upon as a function on the supposition that it is useful in concentrating the salts brought to the leaves, a supposition to which certain workers object on the ground that this assumption carries with it the further assumption that water in the vessels

carries the solutes along with it. These assumptions are held to contradict theory and observation on osmotic movement. The general conception of the function of the xylem is that, in times when water is abundant, it carries the inorganic substances to the leaves; but Atkins finds that sugars are at all times present in the sap of the vessels, usually in greater quantities than the electrolytes. Therefore, the vessels should be regarded as transferring both water and solutes, organic as well as inorganic. This view, however, is opposed to that of Curtis, who suggests that the interposition of living cells across conducting tubes may prevent a flow of solution, and that water may normally flow largely by diffusion.

It has, however, been shown that with the possible exception of *Colocasia* secretions contain both electrolytes and non-electrolytes.

An attempt has been made in this discussion to explain the entrance of water and solutes into the vessels in the presence of root pressure. From a physical point of view it is difficult to conceive why solutes should not be carried with the transpiration current once they enter the vessels. If, in the absence of root pressure, and when there exists a negative pressure in the vessels, water enters the root by filtration, it is also conceivable that soil solutes may also enter along with the water unless some mechanism exists in the root to check their entrance. Curtis, however, holds that there is no flow of solution from the soil into the root, and that the amount of water absorbed bears no relation to the amount of solutes absorbed. Pfeffer states that

A substance imbibed by the cellulose cell walls may reach the center of a tissue without having penetrated a single protoplast. It is indeed possible that the water and salts absorbed by the roots pass mainly, if not entirely, through either the cell walls of living cells or the walls and cavities of dead wood fibers, etc., so that only on reaching the crown of the tree do they penetrate the protoplasts of the actively growing tissues localized there.

If we admit that soil solutes enter the vessels either by filtration or by excretion or both, and are carried to the leaves by the transpiration current, some provision must be conceived to prevent their too great concentration in the leaf cells, otherwise in the course of a transpiring season the leaves would become rigid with salt. Possibly the endodermis may function in controlling the entrance of soil solutes as well as in preventing the backward leakage of water and solutes from the root. Some evidence already exists to support this view, as substances which cannot penetrate the endodermis do not penetrate into the vascular cylinder of the root. In fact, De Ruf de Lavison shows that the suberized walls of endodermal cells are impermeable, that all solutes which enter the vascular cylinder of the root are forced to pass through the protoplasm of the endodermis, and also that cellulose cell walls of the root tip are of such a character that only such solutes enter this region as are able to penetrate the protoplasm. The supposition is, therefore, that the quantity and quality of solutes which penetrate into the root depend upon a sort of filtration across the protoplasm

of the endodermis and that of the root tip. It may be that in the absence of root pressure and in the presence of a negative pressure in the vessels, water and solutes may pass through the endodermis and through the root tip in a purely physical manner. Evidence also exists to support the view that certain amounts of salts are concentrated in the leaves, and it is possible that these salts are thrown out of solution by the protoplasm so as not to upset the osmotic relation of the cells. The assumption that solutes are adsorbed by the living protoplasts accompanying the vessels is also suggestive.

Whatever may be the mechanism of the entrance of solutes into the root and of their passage into vessels, it would appear that the problems here stated are worthy of serious and careful investigation.

DEPARTMENT OF BOTANY,
UNIVERSITY OF WISCONSIN